Combined effect of successive competition periods on population dynamics

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Abstract

This study investigates the effect of competition between individuals on population dynamics when they compete for different resources during different seasons or during different growth stages. Individuals are assumed to compete for a single resource during each of these periods according to one of the following competition types: scramble, contest, or an intermediate between the two. The effect of two successive competition periods is determined to be expressed by simple relations on products of two "transition matrices" for various sets of competition types for the two periods. In particular, for the scramble and contest competition combination, results vary widely depending on the order of the two competition types. Furthermore, the stability properties of derived population models as well as the effect of more than two successive competition periods are discussed.

Keywords: First-principles derivation; Site-based framework; Scramble competition; Contest competition; Resource partitioning; Spatial distribution; Transition matrix

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1 Introduction

Discrete-time population models based on a difference equation have been widely employed for modeling population dynamics in species with seasonal reproduction, but in many cases, these models have been introduced as phenomenological models. Since population dynamics must, in principle, result from behaviors of individuals comprising a population, it is important to clarify the relationships between processes on both individual and population levels (Hassell and May, 1985; Łomnicki, 1988). An effective approach is to derive population models from first principles, and studies of this kind have recently advanced a lot. First-principles derivations are broadly classified into continuous-time approaches (e.g., Gurney, 1998; Wells et al., 1998; Thieme, 2003; Geritz and Kisdi, 2004; Eskola and Geritz, 2007; Eskola and Parvinen, 2007, 2010) and discrete-time approaches (e.g., Royama, 1992; Sumpter and Broomhead, 2001; Johansson and Sumpter, 2003; Brännström and Sumpter, 2005a,b, 2006; Seno, 2007; Anazawa, 2009, 2010). There are also studies employing individual-based simulations (e.g., Johst et al., 2008). Extending the study of Anazawa (2010), which is based on a discrete-time approach, this study investigates the effect of competition on population dynamics when individuals compete for different resources during different seasons or during different growth stages.

It is well known that there are two contrasting types of competition between individuals: scramble and contest (Nicholson, 1954; Hassell, 1975). In scramble, resources are considered to be partitioned evenly, while in contest, resources are monopolized by a few competitively superior individuals. Extending the study of Brännström and Sumpter (2005b), Anazawa (2010) derived a population model for a competition type intermediate between scramble and contest through the consideration of resource partitioning and spatial distribution of individuals, and showed that this model includes various classical population models as special cases in various limits in terms of two parameters. However, this derivation dealt only with cases in which individuals compete for the same resource throughout the competition period, and not with cases in which individuals compete for different resources simultaneously or cases in which variation of resource and competition type depend on seasons or on growth stages of individuals.

Extending the study of Anazawa (2010), this study investigates the effect of competition in situations wherein the overall competition period consists of different competition periods. Individuals compete for a single resource within each period, but the types of resource and competition vary between competition periods. The effect of two successive competition periods is expressed by simple relations on products of two "transition matrices." The results depend on the competition types in the two periods, and in particular, exhibit a great deal of contrast for the scramble and contest competition combination, depending on the order of the two competition types. Further-

1

more, the stability properties of derived population models as well as the effect of more than two successive competition periods are discussed.

2 The basic framework

2.1 Site-based framework

A site-based framework, described below, is assumed as the basic framework for considering the derivation of population models (Sumpter and Broomhead, 2001; Johansson and Sumpter, 2003; Brännström and Sumpter, 2005b; Seno, 2007; Anazawa, 2009, 2010). This is a modified version of the framework used in the study of Anazawa (2010), designed to deal with multiple competition periods. Consider a habitat consisting of n discrete resource sites or patches over which all individuals of a population of size x_t in generation t are distributed. Not moving to other sites, each individual is assumed to compete for resources with other individuals at the same site. As will be described in Section 2.2, the overall period in which individuals compete for resources consists of multiple distinct competition periods, wherein the types of resource and competition depend on these competition periods (Fig. 1). Individuals that procure sufficient resources to grow and survive until the reproductive period, reproduce, and all parents die after the reproductive period. Offspring emerging from each site then disperse and are distributed randomly over the sites again, forming a population in the next generation.

In this situation, the expected population size in generation $t+1$ can be written as follows:

$$x_{t+1} = n \sum_{k=1}^{\infty} p_k(x_t)\,\phi(k). \tag{1}$$

Here, $\phi(k)$, referred to as the interaction function, denotes the expected number of offspring emerging from a site containing k individuals, and its specific forms are determined through the consideration of competition for resources between individuals in a site. On the other hand, $p_k(x_t)$, a function of x_t, denotes the probability of finding k individuals at a given site at the beginning of the overall competition period. Eq. (1) connects population dynamics at two different spatial scales: the population dynamics within each site, represented by $\phi(k)$; and those over the entire habitat consisting of all sites. In this sense, the site-based framework is closely related to scale transition theory (Chesson, 1998a,b; Chesson et al., 2005).

As described in Anazawa (2010), for a situation in which the distribution of individuals shows aggregated patterns, we assume p_k to be the following negative binomial distribution:

$$p_k = \frac{\Gamma(k+\lambda)}{\Gamma(\lambda)\Gamma(k+1)} \left(\frac{x_t}{\lambda n}\right)^k \left(1 + \frac{x_t}{\lambda n}\right)^{-k-\lambda}, \tag{2}$$

2

where λ is a positive parameter, with $1/\lambda$ representing an index of the degree of aggregation. This distribution includes the following Poisson distribution as a special case in the limit as $\lambda \to \infty$:

$$p_k = \frac{1}{k!}\left(\frac{x_t}{n}\right)^k e^{-x_t/n}, \tag{3}$$

which corresponds to a situation in which individuals are distributed completely at random. Here, the number n of the resource sites is assumed to be sufficiently large.

2.2 Competition for resources

We now consider the competition for resources within each site more concretely. Consider that the entire competition period, from the time when individuals enter the site to the beginning of the reproductive period, consists of N distinct competition periods (Fig. 1). Although individuals compete for a single resource during each period, the types of resource and competition depend on the competition period. Letting resource i represent the resource for which individuals compete in period i, each individual is assumed to require an amount s_i of resource i in order to survive until the end of period i and advance to the next period; if an individual alive at the beginning of period i procures the resource amount s_i within this period, it advances to the next period, if not, it dies within period i. Individuals alive at the end of period N advance to the reproductive period and reproduce. Furthermore, the total amount R_i of resource i contained in each site is assumed to follow an exponential distribution with the following probability density function:

$$q_i(R_i) = e^{-R_i/\bar{R}_i}/\bar{R}_i, \tag{4}$$

where $\bar{R}_i$ denotes the mean of R_i. This corresponds to a situation in which the total amount $n\bar{R}_i$ of the resource is partitioned among the n sites completely at random. Distribution of each resource is assumed to be independent.

In period i, the amount R_i of resource i in each site is partitioned between the individuals alive at the site, and the type of resource partitioning is assumed to be one of the following three types, as described in Anazawa (2009, 2010):

(a) **Scramble competition**
    The resource R_i is evenly partitioned between the individuals at the site.

(b) **Contest competition**
    The resource R_i is partitioned between the individuals in the order of competitive ability, i.e., the most competitive one first takes the

3

amount s_i, and then, if the amount of the remaining resource is $\geq s_i$, the next most competitive one takes the amount s_i, and this process repeats until R_i is depleted or all individuals procure s_i.

(c) **Intermediate competition**

This is an intermediate between the above two types. First, a certain amount $\hat{s}_i$ $(< s_i)$ is equally distributed to each individual at the site, and then the remaining resource is partitioned in the order of competitive ability, i.e., the most competitive one first tries to take the amount $s_i - \hat{s}_i$ so as to obtain a total amount s_i. Thereafter, if the amount of the remaining resource is $\geq s_i - \hat{s}_i$, the next most competitive one takes $s_i - \hat{s}_i$, and this process repeats until R_i is depleted or all individuals procure s_i.

Table 1 presents the interaction functions and population models for the three competition types described above when $N = 1$ (Anazawa, 2009, 2010). The six functions defined here are used throughout this study. In this table, $\alpha = e^{-s/\bar{R}}$ and $\hat{\alpha} = e^{-\hat{s}/\bar{R}}$, and β is defined by

$$\beta = \frac{1 - \hat{\alpha}}{1 - \alpha}, \tag{5}$$

representing the degree of deviation from (ideal) contest competition in the case of intermediate competition $(0 < \beta < 1)$. Intermediate competition approaches contest type in the limit as $\beta \to 0$ $(\hat{s} \to 0)$ and scramble type in the limit as $\beta \to 1$ $(\hat{s} \to s)$. As described in Anazawa (2010), the population model $x_{t+1} = f_I(x_t; \alpha, \beta, \lambda)$ for intermediate competition includes the following classical population models as special cases in various limits in terms of β and λ: the Ricker model (Ricker, 1954), the Hassell model (Hassell, 1975; Hassell et al., 1976; De Jong, 1979), the Skellam model (Skellam, 1951), the Beverton-Holt model (Beverton and Holt, 1957), and the Brännström-Sumpter model (Brännström and Sumpter, 2005b).

3 Combined effect of competition periods

3.1 Transition matrix

We now consider how to derive specific forms of $\phi(k)$ for the overall competition period consisting of N distinct periods. Here, we should note that the number of individuals alive at a site can vary with time due to competition. Let $T_{k,m}$, henceforth referred to as the transition probability, be the probability that the number of the individuals alive at a given site changes from k at the beginning to m at the end of the overall competition period; and let T, referred to as the transition matrix, be an infinite size matrix with its (k, m) component given by $T_{k,m}$. The transition probability $T_{k,m}$ can be

written as follows:

$$T_{k,m} = \sum_{l_1=1}^{k} \sum_{l_2=1}^{k} \cdots \sum_{l_{N-1}=1}^{k} T_{k,l_1}^{(1)} T_{l_1,l_2}^{(2)} \cdots T_{l_{N-1},m}^{(N)}, \tag{6}$$

where $T_{k,m}^{(i)}$ denotes the transition probability for period i, i.e., the probability of the number of individuals alive at a given site changing from k at the beginning to m at the end of period i. Eq. (6) can be written concisely in a matrix form as follows:

$$T = T^{(1)} T^{(2)} \cdots T^{(N)}. \tag{7}$$

The interaction function $\phi(k)$ is determined from the transition matrix by using the relation

$$\phi(k) = b' \sum_{m=1}^{k} T_{k,m} m, \tag{8}$$

where b' is a positive parameter representing the average number of offspring produced by an individual alive in the reproductive period multiplied by the survivorship of the offspring until they enter their habitation sites.

3.2 Product of two transition matrices

Next, we determine a product of two transition matrices, which corresponds to the $N = 2$ case of Eq. (6). As will be shown later, products of more than two transition matrices can be determined by recursive use of this result. Given that the competition within period i is the intermediate type specified by $(\hat{\alpha}_i, \alpha_i) = (e^{-\hat{s}_i/\bar{R}_i}, e^{-s_i/\bar{R}_i})$, the transition probabilities for this period are written as follows:

$$T_I(\hat{\alpha}_i, \alpha_i)_{k,m} = \phi_I(\hat{\alpha}_i, \alpha_i)_{k,m} - \phi_I(\hat{\alpha}_i, \alpha_i)_{k,m+1}, \tag{9}$$

where $\phi_I(\hat{\alpha}_i, \alpha_i)_{k,m}$ denotes the probability that at least m individuals survive until the end of period i at a given site where k individuals were alive at the beginning. For the m-th individual, in the order of competitive ability, to be able to obtain the amount s_i of resource so as to survive till the end of the period, $R_i \geq \hat{s}_i k + (s_i - \hat{s}_i)m$ must be satisfied, and hence,

$$\phi_I(\hat{\alpha}_i, \alpha_i)_{k,m} = \text{Prob}[R_i \geq \hat{s}_i k + (s_i - \hat{s}_i)m] I_{k \geq m}, \tag{10}$$

where $I_{k \geq m}$ is defined by

$$I_{k \geq m} = \begin{cases} 1 & \text{(for } k \geq m), \\ 0 & \text{(otherwise).} \end{cases}$$

Determining the probability in the right-hand side of Eq. (10) from distribution (4), and combining the obtained result with Eq. (9), yields the following transition probabilities:

$$T_I(\hat{\alpha}_i, \alpha_i)_{k,m} = \begin{cases} \hat{\alpha}_i^k (\alpha_i/\hat{\alpha}_i)^m (1 - \alpha_i/\hat{\alpha}_i) & (1 \le m \le k - 1), \\ \alpha_i^k & (m = k), \\ 0 & (m \ge k + 1). \end{cases} \tag{11}$$

Substituting the above probabilities with $i = 1, 2$ into Eq. (6), and performing a summation, renders the following relation (for details, see Appendix A):

$$\begin{aligned} T_I(\hat{\alpha}_1, \alpha_1) \, T_I(\hat{\alpha}_2, \alpha_2) \\ = \quad K \, T_I(\hat{\alpha}_1, \alpha_1 \alpha_2) + (1 - K) \, T_I(\alpha_1 \hat{\alpha}_2, \alpha_1 \alpha_2), \end{aligned} \tag{12}$$

where K is a constant $(0 < K < 1)$ defined by

$$K = \frac{\hat{\alpha}_1 - \alpha_1}{\hat{\alpha}_1 - \alpha_1 \hat{\alpha}_2}. \tag{13}$$

This result indicates that the product of two transition matrices of intermediate competition is equivalent to a linear combination of two other transition matrices of the intermediate type. In other words, the effect of overall competition is a linear interpolation of the effects of two distinct intermediate competitions.

Also, combining Eq. (12) and Eq. (8) gives

$$\phi(k) = K \, \phi_I(k \, ; \hat{\alpha}_1, \alpha_1 \alpha_2) + (1 - K) \, \phi_I(k \, ; \alpha_1 \hat{\alpha}_2, \alpha_1 \alpha_2), \tag{14}$$

where ϕ_I is the interaction function for intermediate competition, defined in Table 1. Similarly, the corresponding population model is given by

$$x_{t+1} = K \, f_I(x_t \, ; \alpha_1 \alpha_2, \beta_1, \lambda) + (1 - K) \, f_I(x_t \, ; \alpha_1 \alpha_2, \beta_2, \lambda), \tag{15}$$

where β_1 and β_2 are given, from Eq. (5), by

$$\beta_1 = \frac{1 - \hat{\alpha}_1}{1 - \alpha_1 \alpha_2}, \tag{16}$$

$$\beta_2 = \frac{1 - \alpha_1 \hat{\alpha}_2}{1 - \alpha_1 \alpha_2}. \tag{17}$$

Eq. (15) is a linear combination of two population models for intermediate competition with different values of β. Note that these values of β satisfy $\beta_1 < \beta_2$, since $0 < \alpha_i < \hat{\alpha}_i < 1$ gives $\alpha_1 \hat{\alpha}_2 < \alpha_1 < \hat{\alpha}_1$, and then $1 - \hat{\alpha}_1 < 1 - \alpha_1 \hat{\alpha}_2$.

3.3 Cases of scramble and contest competition

Since the intermediate competition specified by $(\hat{\alpha}_i, \alpha_i)$ approaches scramble in the limit as $\hat{\alpha}_i \to \alpha_i$, and contest in the limit as $\hat{\alpha}_i \to 1$, considering such limits in Eq. (12) gives four other relations involving the transition matrices for scramble and contest, as shown in Table 2. In this table, $T_S(\alpha_i)$ and $T_C(\alpha_i)$ denote the transition matrices for scramble and contest competitions, respectively. Furthermore, these four relations yield similar relations about interaction functions, which then give the corresponding population models for various combinations of scramble and contest competitions shown in Table 3.

In Table 2, it is interesting to note that the product of two transition matrices of the same type of either scramble or contest competition is equivalent to a single transition matrix of the same type. Further, the products of a matrix for scramble and that for contest are different, depending on the combination order of the competition types (discussed further in Section 3.5). Also, note that the set of relations in Eqs. (18)–(21) is mathematically equivalent to the original relation elaborated in Eq. (12), since the latter can be obtained reversely from the former (see Appendix B).

3.4 Emergence of a linear combination

The relation in Eq. (21) in Table 2 indicates that the effect of contest followed by scramble is equivalent to a linear combination of the effects of another contest and another scramble. This relation was derived in a non-intuitive manner, but it is possible to intuitively understand why this linear combination emerges when $s_i/\bar{R}_i \ll 1$, as described below.

For simplicity, we consider the corresponding relation about interaction functions instead of Eq. (21)

$$\phi(k) = \frac{1 - \alpha_1}{1 - \alpha_1\alpha_2}\phi_C(k\,;\alpha_1\alpha_2) + \frac{\alpha_1(1 - \alpha_2)}{1 - \alpha_1\alpha_2}\phi_S(k\,;\alpha_1\alpha_2). \qquad (29)$$

When $s_i/\bar{R}_i \ll 1$, this equation can be approximately written as

$$\begin{aligned}\phi(k) \quad \simeq \quad & \frac{s_1/\bar{R}_1}{s_1/\bar{R}_1 + s_2/\bar{R}_2}\,\phi_C(k\,;\alpha_1\alpha_2) \\ &+ \frac{s_2/\bar{R}_2}{s_1/\bar{R}_1 + s_2/\bar{R}_2}\,\phi_S(k\,;\alpha_1\alpha_2),\end{aligned} \qquad (30)$$

which can be derived as follows. Consider a site with R_1, R_2 resources, and k individuals alive at the beginning. The individuals compete for R_1 in period 1, and for R_2 in period 2. The maximum number of individuals that can live on R_i in period i is given by the maximum integer not exceeding R_i/s_i, which is approximately R_i/s_i when $s_i/\bar{R}_i \ll 1$. This indicates that the overall competition is dominated by the competition with a smaller value

7

of R_i/s_i. In other words, it is dominated by the competition for R_1 (i.e., contest competition) when $R_1/s_1 < R_2/s_2$, and by the competition for R_2 (i.e., scramble competition) when $R_1/s_1 > R_2/s_2$. Hence, the interaction function can be written as follows:

$$
\begin{aligned}
\phi(k) \ \simeq \ & b' \sum_{m=1}^{k} \text{Prob}[m \leq R_1/s_1 < R_2/s_2] \\
& + b' \, \text{Prob}[k \leq R_2/s_2 < R_1/s_1] \, k.
\end{aligned}
\tag{31}
$$

Here, the first term on the right-hand side represents the contribution from the contest competition, which dominates when $R_1/s_1 < R_2/s_2$, with $m \leq R_1/s_1 < R_2/s_2$ being the condition for the m-th individual, in the order of competitive ability, to be able to obtain s_1 from R_1. The second term represents the contribution from the scramble competition, which dominates when $R_1/s_1 > R_2/s_2$, with $k \leq R_2/s_2 < R_1/s_1$ being the condition for all individuals to be able to obtain s_2 from R_2. An explicit calculation using the distribution of R_i, Eq. (4), shows that the first and the second terms on the right-hand side of Eq. (31) are equivalent to the first and second terms of Eq. (30), respectively. The derivation of Eq. (30) provided here explains intuitively why a linear combination of scramble and contest emerges in the $s_i/\bar{R}_i \ll 1$ case.

3.5 Scramble followed by contest vs. contest followed by scramble

Population models (25) and (27) in Table 3 for the combination of scramble and contest depend on the order of these types of competition. In the following, a comparison between these two models is presented. Consider α_s and α_c to be the parameters characterizing scramble and contest competitions, respectively. The model for scramble followed by contest competition (the SC model) is written from Eq. (25) as follows:

$$
x_{t+1} = f_I(x_t\,;\alpha,\beta,\lambda),
\tag{32}
$$

where $\alpha = \alpha_s \alpha_c$ and $\beta = (1 - \alpha_s)/(1 - \alpha)$. On the other hand, the model for contest followed by scramble competition (the CS model) is written from Eq. (27) as follows:

$$
x_{t+1} = \gamma_c \, f_C(x_t\,;\alpha,\lambda) + \gamma_s \, f_S(x_t\,;\alpha,\lambda),
\tag{33}
$$

where $\gamma_s = \alpha_c(1 - \alpha_s)/(1 - \alpha)$ and $\gamma_c = 1 - \gamma_s$. Here, both β and γ_s take values from 0 to 1. Both models approach the model for contest as these parameters approach 0, and the model for scramble as they approach 1. In this sense, both β and γ_s are indices representing the degree of derivation from the model for (ideal) contest competition.

Although both Eq. (32) and Eq. (33) can be regarded as population models intermediate between the models for contest and scramble, they show very different reproduction curves as shown in Fig. 2. When $\hat{x}_t/n \equiv (1-\alpha)x_t/n$ is sufficiently small, models (32) and (33) can be approximately written as

$$\hat{x}_{t+1} \simeq b'\alpha\,\hat{x}_t \left\{ 1 - (1+\beta)\left(1+\frac{1}{\lambda}\right)\frac{\hat{x}_t}{2n} \right\}, \tag{34}$$

$$\hat{x}_{t+1} \simeq b'\alpha\,\hat{x}_t \left\{ 1 - (1+\gamma_s)\left(1+\frac{1}{\lambda}\right)\frac{\hat{x}_t}{2n} \right\}, \tag{35}$$

respectively. This shows that the reproduction curves of the two models with the same value of β and γ_s agree with each other for small values of $\hat{x}_t/n$. However, as $\hat{x}_t/n$ becomes larger, the difference between the two curves increases, and $\hat{x}_{t+1}/n$ approaches 0 for the SC model, and $\gamma_c b'\alpha$ for the CS model. In general, curves of the SC model resemble that of (ideal) scramble competition and curves of the CS model resemble that of (ideal) contest competition. The rationale for such a difference can be explained as follows. When the population size is large, the competition in the first period is severe, thus giving rise to a large reduction in the number of individuals alive in each site. This results in a small impact due to competition in the second period. In this way, the competition in the first period dominates the entire population dynamics when the population size is large.

Next, we compare the stability properties of the two population models. Both models have a positive equilibrium point when $b'\alpha > 1$. Fig. 3 illustrates how the stability properties of the positive equilibrium point depend on $b'\alpha$ and β for $\lambda = 4$. Fig. 3 (a) shows that, for the SC model, the properties of the equilibrium point exhibit an abrupt change with a small increase in β from 0, but Fig. 3 (b) shows that the same is not true for the CS model with a small increase in γ_s from 0. Furthermore, as shown in Fig. 3 (b), the equilibrium point of the CS model is always a point attractor when $\gamma_s < 1/(\lambda + 1)$ (see Appendix C).

3.6 Products of more than two transition matrices

Products of more than two transition matrices can be determined by the recursive use of the relation described in Eq. (12). For example, multiplying both sides of Eq. (12) on the right by $T_I(\hat{\alpha}_3, \alpha_3)$ gives

$$
\begin{aligned}
T_I(\hat{\alpha}_1, &\alpha_1)\, T_I(\hat{\alpha}_2, \alpha_2)\, T_I(\hat{\alpha}_3, \alpha_3) \\
= \ &\{ K\, T_I(\hat{\alpha}_1, \alpha_1\alpha_2) + (1-K)\, T_I(\alpha_1\hat{\alpha}_2, \alpha_1\alpha_2) \}\, T_I(\hat{\alpha}_3, \alpha_3) \\
= \ &K\, T_I(\hat{\alpha}_1, \alpha_1\alpha_2)\, T_I(\hat{\alpha}_3, \alpha_3) \\
&+ (1-K)\, T_I(\alpha_1\hat{\alpha}_2, \alpha_1\alpha_2)\, T_I(\hat{\alpha}_3, \alpha_3). \tag{36}
\end{aligned}
$$

Rewriting the right-hand side with the relation (12) gives

$$T_I(\hat{\alpha}_1, \alpha_1)\, T_I(\hat{\alpha}_2, \alpha_2)\, T_I(\hat{\alpha}_3, \alpha_3)$$

9

$$\begin{aligned}
= \ & K_1 \, T_I(\hat{\alpha}_1, \alpha_1 \alpha_2 \alpha_3) + K_2 \, T_I(\alpha_1 \hat{\alpha}_2, \alpha_1 \alpha_2 \alpha_3) \\
& + \ K_3 \, T_I(\alpha_1 \alpha_2 \hat{\alpha}_3, \alpha_1 \alpha_2 \alpha_3),
\end{aligned} \qquad (37)$$

where

$$K_1 \ = \ \frac{\hat{\alpha}_1 - \alpha_1}{\hat{\alpha}_1 - \alpha_1 \hat{\alpha}_2} \, \frac{\hat{\alpha}_1 - \alpha_1 \alpha_2}{\hat{\alpha}_1 - \alpha_1 \alpha_2 \hat{\alpha}_3}, \qquad (38)$$

$$K_2 \ = \ \left(1 - \frac{\hat{\alpha}_1 - \alpha_1}{\hat{\alpha}_1 - \alpha_1 \hat{\alpha}_2} \right) \frac{\hat{\alpha}_2 - \alpha_2}{\hat{\alpha}_2 - \alpha_2 \hat{\alpha}_3}, \qquad (39)$$

$$K_3 \ = \ 1 - K_1 - K_2. \qquad (40)$$

Eq. (37) indicates that the transition matrix for three successive periods of intermediate competition is equivalent to a linear combination of three transition matrices of intermediate type, which are different from the original ones. The values of β for these intermediate competitions are given by

$$\beta_1 \ = \ \frac{1 - \hat{\alpha}_1}{1 - \alpha_1 \alpha_2 \alpha_3}, \qquad (41)$$

$$\beta_2 \ = \ \frac{1 - \alpha_1 \hat{\alpha}_2}{1 - \alpha_1 \alpha_2 \alpha_3}, \qquad (42)$$

$$\beta_3 \ = \ \frac{1 - \alpha_1 \alpha_2 \hat{\alpha}_3}{1 - \alpha_1 \alpha_2 \alpha_3}. \qquad (43)$$

Note that these values satisfy $\beta_1 < \beta_2 < \beta_3$, which can be obtained from $0 < \alpha_i < \hat{\alpha}_i < 1$.

4   Discussion

In this study, we have considered the effect of competition on population dynamics in a situation that shows dependence of the types of resource and competition on seasons or growth stages. Introducing transition matrices based on the number of individuals alive within a site, we found that the effect of two successive competition periods is summarized in simple relations on products of two transition matrices, as shown in Table 2. Transition matrices for more than two successive periods can be obtained by the recursive use of the relations above, generally resulting in a linear combination of various transition matrices of intermediate competition. In particular, transition matrices for any number of periods of either scramble or contest result in just a single transition matrix of the same competition type. This suggests that the effect of competition in such cases cannot be distinguished from that of competition involving only a single resource.

Three comments on conditions assumed in this study are in order. First, in combining periods of contest or intermediate competition, the resource at each site was assumed be partitioned in the order of competitive ability, but the order in each period was allowed be independent. Thus, we can

10

also consider the order to be determined randomly, i.e., not according to competitive ability, and hence in that case, only fortunate individuals obtain the necessary amount of resource earlier. Second, this study considered only the case in which individuals compete within the same site throughout the overall competition period, but in some species, individuals may compete at different places at different life stages. The results of this study cannot be applied to such situations. Third, for simplicity, simplified assumptions were made in this study. For example, each individual was alway assumed to die if the amount of resource i obtained was smaller than s_i even by a small quantity. Furthermore, no differences between individuals were taken into account, except for their competitive ability. How the results change when we make more realistic assumptions is an issue left to address in future investigations.

Last, a comment on the extension of the results of this study: This study did not consider cases in which individuals compete for multiple kinds of resources simultaneously, but these types of cases can be studied on the basis of the results of the present study. We believe that arguments based on transition matrices and the relationships between them, obtained in this study, can be applied to various situations for studying the effect of competition between individuals on population dynamics.

Acknowledgments

Appendix A

This appendix presents a derivation of Eq. (12), which is an identity on the following product of two transition matrices

$$T_{k,m} = \sum_{l=1}^{k} T_I(\hat{\alpha}_1, \alpha_1)_{k,l} \, T_I(\hat{\alpha}_2, \alpha_2)_{l,m}. \tag{A.1}$$

Because $T_{k,m}$ is expressed similarly to Eq. (9) as

$$T_{k,m} = \phi_{k,m} - \phi_{k,m+1}, \tag{A.2}$$

we first determine $\phi_{k,m}$, which is given by

$$\phi_{k,m} = \sum_{l=1}^{k} T_I(\hat{\alpha}_1, \alpha_1)_{k,l} \, \phi_I(\hat{\alpha}_2, \alpha_2)_{l,m}. \tag{A.3}$$

Here, $\phi_I(\hat{\alpha}_i, \alpha_i)_{l,m}$ is given by

$$\phi_I(\hat{\alpha}_i, \alpha_i)_{l,m} = \hat{\alpha}_i^l (\alpha_i/\hat{\alpha}_i)^m I_{l \geq m} \tag{A.4}$$

11

from Eq. (10), and $T_I(\hat{\alpha}_i, \alpha_i)$ is derived from Eq. (9). Combining these with Eq. (A.3) gives

$$
\begin{aligned}
\phi_{k,m} &= \sum_{l=m}^{k-1} \hat{\alpha}_1^k \Big(\frac{\alpha_1 \hat{\alpha}_2}{\hat{\alpha}_1}\Big)^l \Big(1 - \frac{\alpha_1}{\hat{\alpha}_1}\Big) \Big(\frac{\alpha_2}{\hat{\alpha}_2}\Big)^m \\
&\quad + (\alpha_1 \hat{\alpha}_2)^k \Big(\frac{\alpha_2}{\hat{\alpha}_2}\Big)^m I_{k \geq m}.
\end{aligned}
\tag{A.5}
$$

Rewriting this equation as

$$
\begin{aligned}
\phi_{k,m} &= \frac{1 - \alpha_1/\hat{\alpha}_1}{1 - \alpha_1 \hat{\alpha}_2/\hat{\alpha}_1} \Big\{ \sum_{l=m}^{k-1} \hat{\alpha}_1^k \Big(\frac{\alpha_1 \hat{\alpha}_2}{\hat{\alpha}_1}\Big)^l \Big(1 - \frac{\alpha_1 \hat{\alpha}_2}{\hat{\alpha}_1}\Big) \\
&\quad + (\alpha_1 \hat{\alpha}_2)^k \Big\} \Big(\frac{\alpha_2}{\hat{\alpha}_2}\Big)^m I_{k \geq m} \\
&\quad + \Big(1 - \frac{1 - \alpha_1/\hat{\alpha}_1}{1 - \alpha_1 \hat{\alpha}_2/\hat{\alpha}_1}\Big)(\alpha_1 \hat{\alpha}_2)^k \Big(\frac{\alpha_2}{\hat{\alpha}_2}\Big)^m I_{k \geq m},
\end{aligned}
\tag{A.6}
$$

and performing the summation in the right-hand side gives

$$
\begin{aligned}
\phi_{k,m} &= \frac{\hat{\alpha}_1 - \alpha_1}{\hat{\alpha}_1 - \alpha_1 \hat{\alpha}_2} \hat{\alpha}_1^k \Big(\frac{\alpha_1 \alpha_2}{\hat{\alpha}_1}\Big)^m I_{k \geq m} \\
&\quad + \Big(1 - \frac{\hat{\alpha}_1 - \alpha_1}{\hat{\alpha}_1 - \alpha_1 \hat{\alpha}_2}\Big) (\alpha_1 \hat{\alpha}_2)^k \Big(\frac{\alpha_1 \alpha_2}{\alpha_1 \hat{\alpha}_2}\Big)^m I_{k \geq m}.
\end{aligned}
\tag{A.7}
$$

Further, comparing this equation with Eq. (A.4) renders

$$
\phi_{k,m} = K \, \phi_I(\hat{\alpha}_1, \alpha_1\alpha_2)_{k,m} + (1 - K) \, \phi_I(\alpha_1\hat{\alpha}_2, \alpha_1\alpha_2)_{k,m},
\tag{A.8}
$$

where $K = (\hat{\alpha}_1 - \alpha_1)/(\hat{\alpha}_1 - \alpha_1\hat{\alpha}_2)$. Combining Eq. (A.8) with Eq. (A.2) finally gives

$$
T_{k,m} = K \, T_I(\hat{\alpha}_1, \alpha_1\alpha_2)_{k,m} + (1 - K) \, T_I(\alpha_1\hat{\alpha}_2, \alpha_1\alpha_2)_{k,m},
\tag{A.9}
$$

which yields the relation in Eq. (12).

Appendix B

This appendix privides a description of how Eq. (12) is obtained from the set of Eqs. (18)–(21). First, with Eq. (20), expressing each T_I in the product of two T_I as a product of T_S and T_C gives

$$
\begin{aligned}
&T_I(\hat{\alpha}_1, \alpha_1) \, T_I(\hat{\alpha}_2, \alpha_2) \\
&= T_S(\hat{\alpha}_1) \, T_C(\alpha_1/\hat{\alpha}_1) \, T_S(\hat{\alpha}_2) \, T_C(\alpha_2/\hat{\alpha}_2).
\end{aligned}
\tag{B.1}
$$

Next, rewriting $T_C(\alpha_1/\hat{\alpha}_1) \, T_S(\hat{\alpha}_2)$ in expression (B.1) with Eq. (21) shows that the right-hand side of (B.1) can be written as

$$
\begin{aligned}
T_S(\hat{\alpha}_1) &\left\{ \frac{1 - \alpha_1/\hat{\alpha}_1}{1 - \alpha_1\hat{\alpha}_2/\hat{\alpha}_1} T_C(\alpha_1\hat{\alpha}_2/\hat{\alpha}_1) \right. \\
&+ \left. \left(1 - \frac{1 - \alpha_1/\hat{\alpha}_1}{1 - \alpha_1\hat{\alpha}_2/\hat{\alpha}_1} \right) T_S(\alpha_1\hat{\alpha}_2/\hat{\alpha}_1) \right\} T_C(\alpha_2/\hat{\alpha}_2) \\
&= \frac{\hat{\alpha}_1 - \alpha_1}{\hat{\alpha}_1 - \alpha_1\hat{\alpha}_2} T_S(\hat{\alpha}_1) T_C(\alpha_1\hat{\alpha}_2/\hat{\alpha}_1) T_C(\alpha_2/\hat{\alpha}_2) \\
&+ \left(1 - \frac{\hat{\alpha}_1 - \alpha_1}{\hat{\alpha}_1 - \alpha_1\hat{\alpha}_2} \right) T_S(\hat{\alpha}_1) T_S(\alpha_1\hat{\alpha}_2/\hat{\alpha}_1) T_C(\alpha_2/\hat{\alpha}_2). \qquad \text{(B.2)}
\end{aligned}
$$

Using Eqs. (18) and (19), expression (B.2) can be written as

$$
\begin{aligned}
&\frac{\hat{\alpha}_1 - \alpha_1}{\hat{\alpha}_1 - \alpha_1\hat{\alpha}_2} T_S(\hat{\alpha}_1) T_C(\alpha_1\alpha_2/\hat{\alpha}_1) \\
&\qquad + \left(1 - \frac{\hat{\alpha}_1 - \alpha_1}{\hat{\alpha}_1 - \alpha_1\hat{\alpha}_2} \right) T_S(\alpha_1\hat{\alpha}_2) T_C(\alpha_2/\hat{\alpha}_2). \qquad \text{(B.3)}
\end{aligned}
$$

Finally, with Eq. (20), expressing each $T_S T_C$ in (B.3) as T_I shows that expression (B.3) is identical to the right-hand side of Eq. (12).

Appendix C

From Eq. (33), the slope u of the reproduction curve of the CS model at the positive equilibrium point is written as follows:

$$
u = \frac{b'\alpha}{(1 + y/\lambda)^{\lambda+1}} \left\{ 1 - \gamma_s \left(1 + \frac{1}{\lambda} \right) \frac{y}{1 + y/\lambda} \right\}, \qquad \text{(C.1)}
$$

where $y = (1 - \alpha)x_*/n$, and x_* is the population size at the equilibrium point. Since

$$
\gamma_s \left(1 + \frac{1}{\lambda} \right) \frac{y}{1 + y/\lambda} < \gamma_s(\lambda + 1), \qquad \text{(C.2)}
$$

u is always positive if $1 - \gamma_s(\lambda + 1) > 0$, and hence, the equilibrium point is always a point attractor if $\gamma_s < 1/(\lambda + 1)$.

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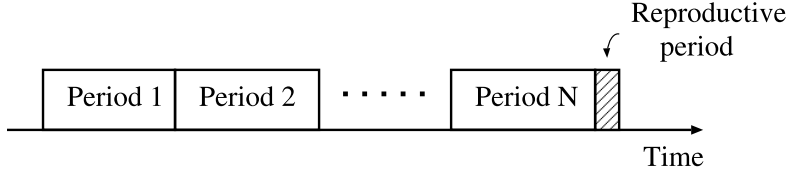
Figure 1: The structure of the overall competition period. The overall competition period consists of N distinct competition periods, where individuals compete for different resources during these different periods.
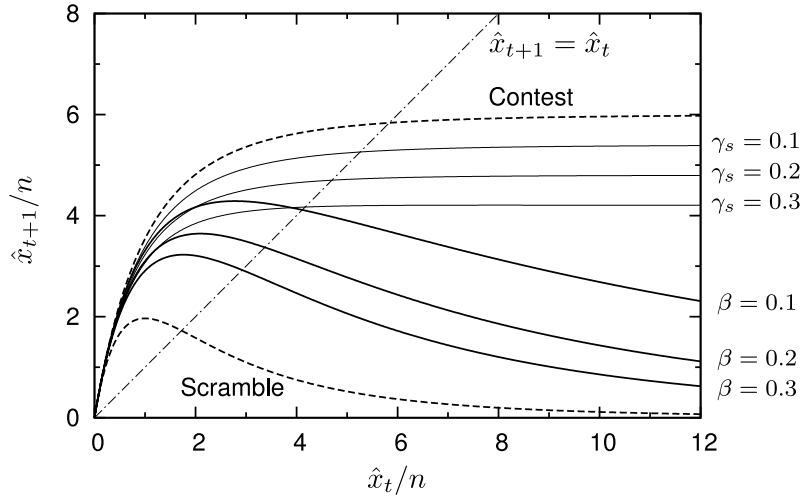

Figure 2: Comparison of reproduction curves of the SC model (scramble followed by contest, thick solid lines) and the CS model (contest followed by scramble, thin solid lines) in the case of $b'\alpha = 6$ and $\lambda = 4$, where $\hat{x}_t = (1 - \alpha)x_t$. Both β and γ_s represent degrees of deviation from (ideal) contest competition. The dashed lines represent the reproduction curves for a single period of contest and for a single period of scramble.
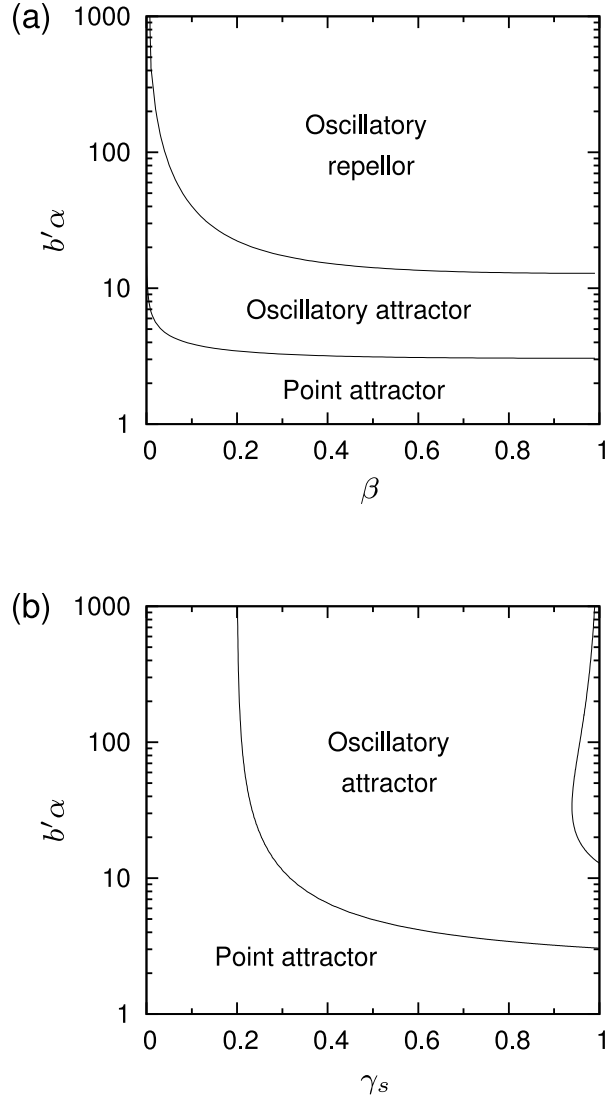
16

Figure 3: Diagrams showing the properties of the positive equilibrium point of (a) the SC model, and of (b) the CS model in the case of $\lambda = 4$. In panel (b), the small region on the right side is the region of the oscillatory repellor.

Table 1: Interaction functions and population models for a single competition period ($N = 1$)

Type	$\phi(k) =$	$x_{t+1} =$
S	$\phi_S(k\,;\alpha) \equiv (b'\alpha)k\alpha^{k-1}$	$f_S(x_t\,;\alpha,\lambda) \equiv (b'\alpha)x_t\left(1 + \frac{(1-\alpha)x_t}{\lambda n}\right)^{-\lambda-1}$
C	$\phi_C(k\,;\alpha) \equiv (b'\alpha)\frac{1-\alpha^k}{1-\alpha}$	$f_C(x_t\,;\alpha,\lambda) \equiv \frac{(b'\alpha)n}{1-\alpha}\left\{1 - \left(1 + \frac{(1-\alpha)x_t}{\lambda n}\right)^{-\lambda}\right\}$
I	$\phi_I(k\,;\hat{\alpha},\alpha) \equiv (b'\alpha)\frac{\hat{\alpha}^k-\alpha^k}{\hat{\alpha}-\alpha}$	$f_I(x_t\,;\alpha,\beta,\lambda) \equiv \frac{(b'\alpha)n}{(1-\alpha)(1-\beta)}\left\{\left(1 + \beta\frac{(1-\alpha)x_t}{\lambda n}\right)^{-\lambda} - \left(1 + \frac{(1-\alpha)x_t}{\lambda n}\right)^{-\lambda}\right\}$

S, scramble competition; C, contest competition; I, intermediate competition.

Table 2: Products of two transition matrices

Type	Relation	
II	$T_I(\hat{\alpha}_1, \alpha_1) T_I(\hat{\alpha}_2, \alpha_2) = \frac{\hat{\alpha}_1 - \alpha_1}{\hat{\alpha}_1 - \alpha_1 \hat{\alpha}_2} T_I(\hat{\alpha}_1, \alpha_1 \alpha_2) + \frac{\alpha_1 (1 - \hat{\alpha}_2)}{\hat{\alpha}_1 - \alpha_1 \hat{\alpha}_2} T_I(\alpha_1 \hat{\alpha}_2, \alpha_1 \alpha_2)$	(12)
SS	$T_S(\alpha_1) T_S(\alpha_2) = T_S(\alpha_1 \alpha_2)$	(18)
CC	$T_C(\alpha_1) T_C(\alpha_2) = T_C(\alpha_1 \alpha_2)$	(19)
SC	$T_S(\alpha_1) T_C(\alpha_2) = T_I(\alpha_1, \alpha_1 \alpha_2)$	(20)
CS	$T_C(\alpha_1) T_S(\alpha_2) = \frac{1 - \alpha_1}{1 - \alpha_1 \alpha_2} T_C(\alpha_1 \alpha_2) + \frac{\alpha_1 (1 - \alpha_2)}{1 - \alpha_1 \alpha_2} T_S(\alpha_1 \alpha_2)$	(21)

II, intermediate followed by intermediate; SC, scramble followed by contest; etc.

Table 3: Population models for two successive competition periods

Type	$x_{t+1} =$	
II	$\frac{\hat{\alpha}_1-\alpha_1}{\hat{\alpha}_1-\alpha_1\hat{\alpha}_2}\, f_I(x_t\,;\alpha_1\alpha_2,\frac{1-\hat{\alpha}_1}{1-\alpha_1\alpha_2},\lambda) + \frac{\alpha_1(1-\hat{\alpha}_2)}{\hat{\alpha}_1-\alpha_1\hat{\alpha}_2}\, f_I(x_t\,;\alpha_1\alpha_2,\frac{1-\alpha_1\hat{\alpha}_2}{1-\alpha_1\alpha_2},\lambda)$	(22)
SS	$f_S(x_t\,;\alpha_1\alpha_2,\lambda)$	(23)
CC	$f_C(x_t\,;\alpha_1\alpha_2,\lambda)$	(24)
SC	$f_I(x_t\,;\alpha_1\alpha_2,\frac{1-\alpha_1}{1-\alpha_1\alpha_2},\lambda)$	(25)
	$\frac{(b'\alpha_1\alpha_2)x_t}{[1+(1-\alpha_1)x_t/n][1+(1-\alpha_1\alpha_2)x_t/n]}$ (for $\lambda=1$)	(26)
CS	$\frac{1-\alpha_1}{1-\alpha_1\alpha_2}f_C(x_t\,;\alpha_1\alpha_2,\lambda) + \frac{\alpha_1(1-\alpha_2)}{1-\alpha_1\alpha_2}f_S(x_t\,;\alpha_1\alpha_2,\lambda)$	(27)
	$(b'\alpha_1\alpha_2)\, x_t\, \frac{1+(1-\alpha_1)x_t/n}{[1+(1-\alpha_1\alpha_2)x_t/n]^2}$ (for $\lambda=1$)	(28)

II, intermediate followed by intermediate; SC, scramble followed by contest; etc.